

WAR AS A SYSTEM IN NATURE

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Examples of ant colonies fighting “wars” have long been known, but the relationship between ant wars and human wars has been generally left as a loose analogy.

Here, we take the relationship seriously. First, we show that “ant wars” are mass, organized, mutual, and lethal conflict between communities, and hence that current definitions of human wars encompass ant wars.

Second, we survey the remarkable variety of characteristics that ant war share with human war. We show that neo-realist international relations, sociological in-group/out-group distinctions, the psychology of mobilization and behavioural norms, technological innovation, diplomacy, intelligence gathering, social specialization, and the militarized state all accompany ant wars just as they accompany human wars. We conclude that war is a single system hosted in these very different animals.

We suggest applications of this perspective, with a particular focus on current debates about whether war and peace should be viewed as distinct domains, or simply as points on a “spectrum of conflict” bracketing “grey zones” that are neither one nor the other.

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1. INTRODUCTION

Entomologists have long looked to human societies and events to help them understand the world of insects. They have spoken for more than a century of “wars” between insect colonies³ and, to describe what happens during these wars, they have imported a rich military vocabulary. Terms such as “armour,” “weapon,” “battle,” “warrior,” “soldier”, “phalanx”, “bivouac”, “kamikaze”, and “mercenary” all appear in insect research.

There has been much less traffic in the opposite direction. It is true that “insect wars” have become increasingly familiar to us through television and YouTube, often narrated by the mellow tones of David Attenborough, but scholars of human wars still view their subject as unique to our species.

³ see, for example, William Morton Wheeler, *Ants: Their Structure, Development, and Behavior* (The Columbia University Press, 1910).

As just one example: October 2020 saw the publication of Margaret MacMillan's book *War: How Conflict Shaped Us*,⁴ based on her 2017 Reith Lectures. As epigraph for the Introduction she chose a quotation from Svetlana Alexievich: "War remains, as it has always been, one of the chief human mysteries".⁵ For Chapter 1 she chose a quotation from Frederic Manning: "War is waged by men; not by beasts, or by gods. It is a peculiarly human activity."⁶

Why have scholars of human war ignored insect wars? We can think of several reasons:

- Caution. Schooled in the humanities or social sciences they may be reluctant to venture into the study of animal behaviour, and especially reluctant to project human forms, emotions and ideas onto other creatures, portraying these creatures in ways that suit particular human agendas.
- The spectre of "biological determinism" and social Darwinism. The sociobiological application of natural selection to explain aspects of human societies caused great controversy in the 1980's and leads uncomfortably close to saying "war is in our genes". If war is claimed as a widespread reality in nature, fashioned unalterably into the bodies and minds of living beings, is this to say that human beings are fated to be entangled in war forever?
- The obvious distance between individual humans and insects on the evolutionary tree. Can creatures as unintelligent and tiny as ants really participate in actual war? Surely this is all just a matter of convenient metaphor? If we were to find war among chimpanzees, our evolutionary cousins, that would be one thing, but among insects?
- The question, "so what?" Even if we conclude that insects do engage in war, of what possible use is that to those of us concerned with human history and human action, which are surely varied and complex enough by themselves?

This essay takes seriously the idea that speaking of "insect wars" is not just metaphor or imagery. It argues that insect war and human war can usefully be thought of as instances of the same thing, developing in response to similar forces. It makes the following claims:

⁴ Margaret MacMillan, *War: How Conflict Shaped Us* (Allen Lane, 2020).

⁵ Svetlana Alexievich, *The Unwomanly Face of War* (Penguin Random House, 2018), <https://www.penguinrandomhouse.com/books/540744/the-unwomanly-face-of-war-by-svetlana-alexievich/>.

⁶ Frederic Manning, *The Middle Parts of Fortune: Somme and Ancre, 1916* (Vintage Classics, 2014), <http://gutenberg.net.au/ebooks02/0200261.txt>.

- Definitions of “war” either fit insect wars or can be extended to do so without damage to their meaning. There are no reasonable grounds for the assertion that wars are uniquely human events.
- Acknowledging that “insects fight wars” focuses attention on war as a system, emphasizing that wars (as discrete events) are inextricably linked to the organization of societies so as to fight wars effectively.
- Beyond the basic definition of war, many questions that we ask about human wars are also asked of insect wars and many concrete features of human war can also be found in insect wars. We believe there are opportunities for learning in both directions, and suggest some possible avenues.

Preliminaries

Many families of insect fight wars, including ants, termites, bees, and wasps. This essay focuses on ants (*Formicidae*), a taxonomic *family* that taxonomists classify into 21 *subfamilies*, each of which is divided into a number of *genera* (300 in all), each of which contains a number of *species*. Over 15,000 species are known⁷ with several thousand still to be classified.⁸

Many ant species live in colonies comprised of a single nest. The colony is populated by a single *queen*, many female *workers*, and sometimes a few males. The workers are the product of fertilized eggs and so are genetically “half-sisters”, to import an androcentric term. The males are the product of unfertilized eggs, live only for long enough to take part in mating with a new queen, and then die.

Ant societies are *eusocial*, meaning that the eggs and larvae, which together comprise the *brood*, are cared for by non-reproductive individuals, not by biological parents in a family unit. In ants, those individual carers are the female workers.

In many species of ant, a queen founds a new colony by selecting a nest location and starting to lay eggs. For many ant species, such as those of the subfamily *Ponerine*, a colony consists of only a few tens or hundreds of ants. For others, colony populations may grow to the millions.

⁷ Benoit Guénard, “The Global Ant Biodiversity Informatics (GABI) Database: Synthesizing Data on the Geographic Distribution of Ant Species (Hymenoptera: Formicidae),” *Myrmecological News* 24 (March 2017): 83–89.

⁸ Florian Steiner, “How Many Ant Species Are There on Earth?,” *Myrmecological News Blog* (blog), June 15, 2018, <https://blog.myrmecologicalnews.org/2018/06/15/how-many-ant-species-are-there-on-earth/>.

Individual worker ants may live only a year or two, but the colony lives as long as the queen continues to lay eggs, which in some species may be 20 or 30 years. In this time, the colony goes through a lifecycle. When young, the focus of its activities is caring for the brood; as the colony grows, it spends more energy foraging farther afield. When the queen dies, so does the colony.

The queen/worker distinction is almost universal in ants, but worker ants in large colonies may further divide into “physical worker subcastes”⁹ of distinct sizes: minor workers, major workers (also called “soldiers”) and, in five genera, “supermajors”. About one in six genera of ants have species with these anatomical subcastes. The genus *Pheidole* consists of over 650 species distributed around the world, many of which are ecologically important where they live, and all of which have large-headed soldier castes.¹⁰

The variety of ant behaviour seems endless. Some species have multiple queens in a single nest; in others some worker ants lay eggs; others yet live in “supercolonies”, comprising many nests and many queens. Most colonies are tied to a specific location, but 200 species of “army ant” have no permanent nesting site. When we talk, below, of “ant war” this is not a single universal phenomenon, but a variety of behaviours that have emerged, in some cases many times independently.

Still, some generalities are useful. To paint with a broad brush, “For both ants and humans, the propensity to engage in true warfare is related at least in a rough way to the size of a society”.¹¹ Moffett observes that small colonies “seldom conduct protracted battles”, modestly-sized societies of a few thousand are “judicious about jeopardising their troops”, and “full bore conflicts appear to be most common for ant species with mature colonies composed of hundreds of thousands of individuals or more.”

2. WHAT MAKES A WAR?

It has long been recognized that ants display behaviour that looks like war. Here is Henry David Thoreau in 1854:

One day when I went out to my wood-pile, or rather my pile of stumps, I observed two large ants, the one red, the other much larger, nearly half an inch long, and black, fiercely contending

⁹ Bert Hölldobler and Edward O. Wilson, *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies* (W. W. Norton & Company, 2008), 134, <https://wwnorton.com/books/9780393067040>.

¹⁰ Hölldobler and Wilson, 145.

¹¹ Mark W. Moffett, “Ants & the Art of War,” *Scientific American* 305, no. 6 (2011): 84–89.

*with one another. Having once got hold they never let go, but struggled and wrestled and rolled on the chips incessantly. Looking farther, I was surprised to find that the chips were covered with such combatants, that it was not a duellum, but a bellum, a war between two races of ants, the red always pitted against the black, and frequently two red ones to one black. The legions of these Myrmidons covered all the hills and vales in my wood-yard, and the ground was already strewn with the dead and dying, both red and black*¹².

Is this really a “war” or is Thoreau just seeing a surface similarity? Identifying what counts as war and what does not is not just a matter for dictionaries. In most societies intentional killing is forbidden under normal circumstances, but is permitted, even required, and often lionized if it takes place in war. Over millennia, humans have repeatedly separated war from the everyday activities of society, often by means of symbolic acts and ceremonies, so that the norms of the battlefield do not spill over into civilian society.

Margaret MacMillan identifies, in the early pages of *War*, a set of attributes associated with war. Here we show that conflicts between insect societies have these attributes.

Mass violence

“War” writes MacMillan “is distinguished from a bar fight by its scale and its organization. War involves dozens, hundreds, thousands, even millions rather than one or a few people committing violence on each other.” A discussion of organization is postponed to later in this section: let’s first address scale.

Thoreau is just one of many observers who have remarked on the scale of ant conflicts. We shall encounter cases below where deaths may number in the thousands, or even the millions. Here we quote just one more historical observation: more than 80 years ago,¹³ Auguste Forel encountered battles between colonies of *Tetramorium caespitum* (Pavement ants) in Switzerland. A battle in Zurich had a front of more than 30 metres where, as the ants

¹² Henry David Thoreau, “Chapter 12: Brute Neighbors,” in *Walden; or, Life in the Woods* (Boston: Ticknor and Fields, 1854), <https://americanliterature.com/author/henry-david-thoreau/essay/the-battle-of-the-ants>.

¹³ André Parent, “Auguste Forel on Ants and Neurology,” *Canadian Journal of Neurological Sciences / Journal Canadien Des Sciences Neurologiques* 30, no. 3 (August 2003): 284–91, <https://doi.org/10.1017/S0317167100002754>.

employed their toxic stings, “thousands of dead bestrewed the ground.” “These wars that I watched,” he said, “lasted more than a month.”

The involvement of thousands of combatants on each side qualifies ant wars as “mass violence”.

Lethal violence

Acknowledging the centrality of death, MacMillan writes “War would not be possible without our willingness to kill” (p6). Without death-dealing by the contending parties there may be contest, conflict, violence and so on, but there will not be war.

Since Jane Goodall’s study of chimpanzees in Gombe,¹⁴ researchers have sought forms of primitive war among animals closely related to humans. But the most they have produced are organized, small-scale, minimally lethal raids with low lethality (in the tens) partly because the genus *pan* is, in its natural endowments, only slightly more fitted for lethal action than human beings.

Humans overcome this obstacle to slaughter through the invention of lethal weapons and strategies. Many definitions of war among humans do not refer directly to lethality, but refer instead to “armed” conflict.

Ants have their own sources of lethality. These may not be weapons in the distinctively human sense—tools or devices separate from the body and extending its functions. Instead, they are organic, not prosthetic, and may include anatomical features such as outsize mandibles (notably in the genus *Pheidole*) or chemical weapons, such as stings, sprays, or foams.¹⁵ These organic weapons, combined with an array of lethal behaviours, can make ant engagements more deadly than those of any non-human mammal.

Violence between communities

MacMillan writes that “[War] is a clash between two organized societies which command the adherence of their members and have existed over considerable time, usually in their own territory... Violence is not war unless it is carried out in the name of a political unit... directed against another political unit”.

¹⁴ Jane van Lawick-Goodall and David A. Hamburg, “Recent Developments in the Study of Primate Behavior,” *Bulletin of the American Academy of Arts and Sciences* 27, no. 7 (1974): 36–48, <https://doi.org/10.2307/3823704>.

¹⁵ Ulrich Maschwitz, Karla Jessen, and Eleonore Maschwitz, “Foaming in Pachycondyla: A New Defense Mechanism in Ants,” *Behavioral Ecology and Sociobiology* 9, no. 1 (August 1, 1981): 79–81, <https://doi.org/10.1007/BF00299857>; A. Buschinger and U. Maschwitz, “Defensive Behavior and Defensive Mechanisms in Ants,” in *Defensive Mechanisms in Social Insects* (Hermann, H. R., Ed) (New York: Praeger, 1984), 95–150.

We think of these “political units” as coherent bodies. International relations scholars speak of nation states acting as if they have interests, take action, and act with intent.

Ant colonies also have interests above and beyond those of their member organisms: resources, nesting sites, a functioning labour force, the survival of the next generation, and a territory that is considered its own. Like nation states, ant colonies will fight to defend or expand those interests, the interests of individual soldiers themselves being of little consequence in comparison to the whole.

Territorial ants must preserve the integrity of their boundaries. Species that practice agriculture may live or die along with their food source. Both will fight aggressors to defend what matters to their colony.¹⁶ “The colony is the unit of meaning in the lives of ants. The workers’ loyalty to it is nearly total”.¹⁷ The level of cohesion is such that, for a century, people have spoken of an ant colony as a “superorganism”. The collective pursuit of such social ends is surely the heart of politics.

Extending the concept of “violence between communities” to ants does require one specific jump. *Homo sapiens* is the sole surviving species in the genus *homo*, so human wars are all among communities of a single species. If humans engage in mass fatal violence against another species (applying insecticide to crops, for example), we do not usually think of it as war, except perhaps as a loose metaphor. In contrast, ant colonies engage in mass, organized, lethal conflict with colonies of other species. Thoreau referred to “races” of red and black ants in his woodlot, but we know that these are different species. There is even large-scale mutual violence between ants and termites, which belong to an entirely different taxonomic order (*blattodea*).¹⁸ Can we still use the term “war” to describe these conflicts?

We believe that we can. There were once other species within the genus *homo*, such as *homo neanderthalensis*: we might use the term “war” if a community of one of these species was in a violent clash with a community of *homo sapiens*. We accept the non-metaphorical use of the term “war” to describe fictional hostilities with aliens from other planets if the enemies have

¹⁶ Bert Hölldobler and Edward O Wilson, *The Leafcutter Ants: Civilization by Instinct* (W. W. Norton & Company, 2011).

¹⁷ Bert Hölldobler and Edward O. Wilson, *Journey to the Ants: A Story of Scientific Exploration* (Belknap Press, 1998), Preface, <https://www.hup.harvard.edu/catalog.php?isbn=9780674485266>.

¹⁸ William Morton Wheeler, “Ecological Relations of Ponerine and Other Ants to Termites,” *Proceedings of the American Academy of Arts and Sciences* 71, no. 3 (1936): 159–243, <https://doi.org/10.2307/20023221>.

a form of intelligence similar to our own, regardless of how morphologically different they might be; *War of the Worlds* for example. If you accepted Tolkien's use of "war" to describe conflicts among elves, dwarves, men, orcs, ents, and so on, then you have already accepted the principle.

Mutual violence

MacMillan writes of war as a "clash between two organized societies", and the word "clash" carries with it the implication of violence in both directions. We speak of war when there is a level of symmetry between the sides that enables mutual violence. When the violence is one-sided, we may speak of raids, attacks, slaughter, or massacre, but we will not be too quick to talk of war.

Even among humans, the symmetry is never exact. Each side of a war is perpetually seeking advantage, which is to say seeking asymmetry. The clashing communities may employ different weapons, different tactics, different modes of organization, but mutuality remains in that each has a way to fight against the other—violence goes both ways, or at least has the potential to do so.

Mutuality is built into our understanding of war at the individual level as well. The soldier kills, but also risks death. Much of the mystique of war lies in this individual mutuality: without the risk of death there is no heroism, no bravery, no honour in killing. And while, again, each side may seek to minimize its own casualties and minimize the risk to its own soldiers, rules of war seek to restrict war-fighting to mutual violence, for example by outlawing risk-free killing of non-combatants.

We have already seen examples of mutual violence between ant colonies. Ants, like humans, also engage in one-sided mass, organized, lethal violence against others that is not mutual. "Army ants" is the collective name for hundreds of ant species that do not construct permanent nests, but which are perpetually on the move. Army ants search for food in massive numbers, and may consume up to half a million prey animals per day. The prey species vary, and may include worms, larvae of other insects, and occasionally eggs of vertebrates. But while the use of army terminology has been imported, the actual violence is called "predation" or "foraging" and not "war fighting" because the prey is so different from the hunter. The violence is not mutual.

Organized violence

Finally, it is time to confront the question of organization, the coordination of individual organisms so as to accomplish a goal. “War in its essence is *organized violence*”, says MacMillan (emphasis added).¹⁹

Ants organize at several scales to better fight wars. At a small scale, they demonstrate “team work”. Thoreau observed that several red ants would act together to kill a black ant, and it is common for ants to act in “teams” during conflict. For example, some *Pheidole* ants act as a team when confronting intruders: a group of several “minors” will pin down the intruder and recruit a major, with larger and stronger mandibles, to decapitate her.²⁰

Larger scale coordination takes place during recruitment for war fighting. An ant of a slave-taking species (of which more below), traveling outside her immediate territory, encounters the nest of a slave species.²¹ She returns at once to her own nest, where she recruits other ants of her colony for a joint enterprise. Having assembled, they proceed together to the target. They may follow a chemical trail laid down by the scout or she may physically lead them (that is, travel at the head of a column). The slave-takers invade, may engage in extensive, lethal battles with those who resist them, and carry the young (larvae and pupae) back to their home, where the slaves are raised to take care of the slave-takers. In this sequence of actions, raiders encounter obstacles in their journeys, solve problems, and make group decisions. Moreover, they may return to the raided domicile several times, apparently remembering that there are larvae and pupae still to be taken. There is no map, there are no generals with pointers, but surely there is “evidence of the coordination of the movements of individuals in such a way as to accomplish a goal.”

At an even larger scale, ant armies and societies display organization in the form of specialization and coordination to better fight wars.

Hölldobler and Wilson²² refer to “organized conflict among colonies.” We believe this description is justified.

¹⁹ MacMillan, *War*, xiv.

²⁰ Carl Anderson and Nigel R. Franks, “Teams in Animal Societies,” *Behavioral Ecology* 12, no. 5 (September 1, 2001): 534–40, <https://doi.org/10.1093/beheco/12.5.534>.

²¹ Edward O. Wilson, “Slavery in Ants,” *Scientific American* 232, no. 6 (1975): 32–40; Bert Hölldobler, “Tournaments and Slavery in a Desert Ant,” *Science* 192, no. 4242 (May 28, 1976): 912–14, <https://doi.org/10.1126/science.192.4242.912>.

²² *The Ants* (Harvard University Press, 1990).

Definitions of war

For the purposes of this article, we define a war as *mass, organized, mutual, and lethal conflict between communities*.

We do not intend this to be an exclusive definition, but do claim that it is a reasonable definition consistent with generally-accepted ideas while avoiding an artificial restriction to humanity. The Stanford Encyclopaedia of Philosophy defines wars as “large-scale armed conflicts between organized groups”.²³ Jack Levy observes that “International relations theorists generally define war as large-scale organized violence between political units”.²⁴

3. WAR AS A SYSTEM

It is remarkable that ants, so different from humans, fight wars, yet a common definition of war is of limited interest. When we talk of human wars, we do not seek simply to classify events as “war” or “not-war”; we want to know how wars come about, what effects they have, how they can be avoided or limited, and how they are won and lost. Addressing these questions leads us inevitably to the worlds of international relations, social institutions, ethics, human nature, the nation state, technological innovation, law, diplomacy, and more. Wars are not merely events that erupt at random times and places: they are the visible, above-water part of a much bigger iceberg, inextricably connected to these other realms of nation states, ethics and so on, and these realms seem uniquely human. Together, we may call wars (the events) and those other heterogenous realms that they are connected to, a *war system*. We may think of the system as being in a “hot state” when a war is being fought, and in a “cold state” between wars. The violence might not be there, but all the elements that it is connected to are still in evidence.

MacMillan does not use the term, but she treats war as a system in that she traces how war (events) shape and are shaped by other entities. Her book’s subtitle is *How Conflict Shaped Us*, and she pursues the theme throughout Chapter 1. She quotes historian and sociologist Charles Tilly’s well-known aphorism that “War made the state and the state made war”²⁵ and traces the

²³ Seth Lazar, “War,” in *The Stanford Encyclopedia of Philosophy*, ed. Edward N. Zalta, Spring 2020 (Metaphysics Research Lab, Stanford University, 2020), <https://plato.stanford.edu/archives/spr2020/entries/war/>.

²⁴ Jack S. Levy, “The Causes of War and the Conditions of Peace,” *Annual Review of Political Science* 1, no. 1 (1998): 139–65, <https://doi.org/10.1146/annurev.polisci.1.1.139>.

²⁵ *War*, 20.

growth of centralized state power in Europe by the 18th century (p23) to the wars of that time.

As MacMillan emphasizes, the war system is not tied to any particular form of political organization; it has made its home in many different human societies throughout history. When feudalism is replaced by capitalism, with attendant political transformations, war may be transformed but it marches on. When capitalism is displaced or modified by socialistically inclined states, war changes but continues. None of this means it cannot be constrained or defanged, but it does suggest that human war itself is a complex, adaptable entity with its own nature.

But surely this picture of a war system is quintessentially about us as humans? Even if ant conflicts fall under a definition of “war” can we learn anything from them about the questions we really want to ask? We suggest that the answer is “yes”. The *formicidae* do not hand out medals to victorious heroes or sit at negotiating tables any more than they wave tiny flags as they rush into battle, but many of the connected phenomena that form the human war system have their own parallels in the insect world. War, we suggest, is a system in nature, which is hosted in both ants and humans.

The war system is an example of convergent evolution, that is, the independent appearance of similar complex features in different contexts. The eye is an example of convergent biological evolution, having developed independently along multiple separate branches of the evolutionary tree. We can say that eyes are *hosted* in many species. The city is an example of convergent social evolution, which became hosted in independent civilisations, as this passage from Ronald Wright, quoted by Gowdy and Krall, beautifully illustrates:²⁶

What took place in the early 1500s was truly exceptional, something that had never happened before and never will again. Two cultural experiments, running in isolation for 15,000 years or more, at last came face to face. Amazingly, after all that time, each could recognize the other's institutions. When Cortés landed in Mexico he found roads, canals, cities, palaces, schools, law courts, markets, irrigation works, kings, priests, temples, peasants, artisans, armies, astronomers, merchants, sports, theatre, art, music, and books. High civilization, differing in

²⁶ John Gowdy and Lisi Krall, “The Economic Origins of Ultrasociality,” *Behavioral and Brain Sciences* 39 (ed 2016), <https://doi.org/10.1017/S0140525X1500059X>.

*detail but alike in essentials, had evolved independently on both sides of the earth.*²⁷

Using the word "eyes" to name the octopus's organ of vision is not just a metaphor for mammalian eyes, and use of "city" to describe Tenochtitlán is not just a metaphor for European cities. In both cases, a common underlying dynamic generates a similar outcome in different environments. In both cases, the processes are broadly evolutionary, in the sense that we would not say that cities cause roads or that roads cause cities, but that each is necessary for and accompanies the other. In the same way, the system of war is caused by and causes large-scale complex societies, be they human or insect.

Wars in humans and ants are not identical in all cases, any more than an octopus eye is identical to a human eye, but many essential features of the war system are displayed in many of those environments in which it is hosted, be they human or ant.

A brief history of an idea

Thinking of war as a system is not a novel idea. Among academic social sciences, the sociological perspective is perhaps the most system-oriented, but the first reference that we have found is in the work of the 19th century English Quaker Jonathan Dymond.

Members of the movement for peace in Dymond's time used a variety of terms to carry out a program of defamiliarization of war. They wanted people to see war in a new light, and to this end pictured it in innovative ways. For example, they referred to war as a "custom"—a primitive custom that was comparable to human sacrifice and slavery and should, like those customs, be abolished. "System," as employed by Dymond, took its place as one of the agents of defamiliarization.

Far from being deterministic thinkers, these intellectuals affirmed that war is not implanted unchangeably in the nature of human beings, that humans are not fated to be entangled in war forever. The conviction that war is merely a custom or system and could be abolished was fuelled by the direct participation of many of these intellectuals in the movement to abolish another custom or system in their time, namely slavery.

By the 1930s the expression "war system" appears to have become quite common. In *Merchants of Death*, an important 1934 work on the arms industry, Engelbrecht and Hanighen assumed their readers would be familiar

²⁷ Ronald Wright, *A Short History of Progress* (Toronto: House of Anansi Press Limited, 2004), 50, <https://houseofanansi.com/products/a-short-history-of-progress>.

with it. "One may be horrified," they said, "by the activities of an industry which thrives on the greatest of human curses; still it is well to acknowledge that the arms industry did not create the war system. On the contrary, the war system created the arms industry" [p7]. Of course, as with the early 19th century writers, Englebrecht and Hanighen used the term "system" to refer to a human system—they did not have other species in mind. Like the earlier writers, they used the term to make war more visible and more vulnerable to criticism.

Not long after *Merchants of Death* was written a more complex and ambitious concept of system began to be worked out by the creators of general systems theory. Intellectuals such as Anatol Rapoport and Kenneth Boulding, who participated over the following decades in the building of systems theory, were involved in the development of peace studies, so it is not surprising that a systems view of war became common—though never universal—among participants in peace studies.

Entomologists, taking an evolutionary perspective, implicitly treat ant wars as systems. From an entomologist's perspective, explanations take the form of symbiotic relations between warfare and the social structures or physical structures required to fight it. In both ants and humans, armies make war, and wars make armies. It makes no more sense to analyse the causes of wars without asking about army formation than to study predators without prey, or supply without demand. Studies that examine only the wars themselves inevitably miss much and are unreliable as predictors of the future of war.

The identification of systems often thought of as human in ants is also not new. Here are some other systems that have been observed in both ants and humans.

Agriculture as a system in nature

The development of agriculture, and social complexity, in ants and humans has been driven, some suggest, by similar forces.²⁸ In both ants and humans, the development of agriculture meant that species could produce their own food, and accompanied the development of larger, fixed communities built around their crops. Hölldobler and Wilson have said: "Both human civilization and the evolution of extreme insect superorganisms were attained by agriculture, a form of mutual symbiosis of animals and plants or fungi."²⁹

²⁸ Gowdy and Krall, "The Economic Origins of Ultrasociality."

²⁹ Hölldobler and Wilson, *The Ants*, 408.

Humans have been farming for about 12,000 years, but compared to some species of ant we are mere novices. More than two hundred species of ant in the Americas belonging to the *Attini* tribe have engaged in “industrial-scale” fungus farming (or ant-fungus symbiosis) for over 50 million years.³⁰ Prominent among these are the “leafcutter” ants of the Amazon basin,³¹ which build communities with millions of individual members cooperating within large, complex domiciles with “hundreds of interconnected fungus garden chambers”.³² They prepare fungus gardens assiduously through a multi-phase process, manuring and weeding the gardens while removing parasitical growths that could ruin the crop and damage the health of the colony. They choose, cut, and transport plant materials to the domicile, to provide a growth medium for the food of the colony. They put specialized defence procedures in place to protect the workers returning with the plants. There is extreme morphological specialization in this system, with ants of quite different sizes and shapes—though of the same species and colony—performing separate tasks. This agricultural system has transformed the fungus so that it no longer exists in the wild but is unique to ant gardens: the ants have become dependent on their crop, which in turn provides the nutritional basis for their colony.

It is possible that, in both humans and ants, the need to lay claim to property, and the time lag between planting and harvesting, created the need for armies, and that larger societies which developed war-making innovations (including division of labour) were better placed to survive as larger societies encroached on each other’s territories.³³

Nomadism as a system in nature

Certain species of ants subsist in whole or in part on the exudations of other insects—aphids, for instance. They tend these creatures. They protect their herds from predators, build shelters for them, move them to new pastures, “milk” them, and so on. The herd creatures may themselves undergo morphological changes to suit their altered lifestyle: as with fungus farmers the relationship may be symbiotic, involving mutual adjustment and mutual advantage.

³⁰ Sanne Nygaard et al., “Reciprocal Genomic Evolution in the Ant-Fungus Agricultural Symbiosis,” *Nature Communications* 7, no. 1 (July 20, 2016): 12233, <https://doi.org/10.1038/ncomms12233>.

³¹ Hölldobler and Wilson, *The Leafcutter Ants: Civilization by Instinct*.

³² Hölldobler and Wilson.

³³ Gowdy and Krall, “The Economic Origins of Ultrasociality.”

Maschwitz and Hänel³⁴ have been precise when using the word “nomadism” to refer to this phenomenon in Malayan ants. “Nomads,” they say, “are stock farmers who subsist from their livestock and who closely coordinate their life style with that of their livestock, for instance, by following them to the pastures these need.” They then explain how “the migrating herdsman *Dolichoderus*,” a species of ant, fits this definition. These authors are not claiming mere resemblances, nor are they dealing in metaphor. They wish to say that *Dolichoderus* is nomadic. That is, there is a system in nature, nomadism, that is hosted by certain species of ant and is likewise hosted by certain societies and cultures within the species homo sapiens.

Slavery as a system in nature

The literature of myrmecology has made reference for well over a century to slavery among ants. “Slaves” and “slave-taking” are common terms in the literature (although Herbers has suggested the use of “piracy” instead of “slavery”³⁵). Yet social scientists and historians who set out to study human slavery usually feel no obligation to mention ants. Slavery, they appear to feel, is a uniquely human institution. No doubt ownership, if this is to be considered essential to slavery, cannot be proved and has, probably, no clear meaning among ants. But extreme forms of domination are found, and they include the appropriation of the labour power of the subordinate.

“Slave-taking” ant colonies seek out and raid targeted colonies, take members of the targeted colony by force to their domicile, and raise them as subordinate providers of labour, assigning them tasks such as cleaning, feeding and otherwise tending to the members of the dominant’s colony. In some instances, the raiders become so specialized in the art of slave-taking that they lose the ability to perform the basic maintenance tasks of their political unit (the slavery is called in this case, “obligate”). If they are deprived of their captured labourers their colony may decline or even disintegrate.

Where the captured ants are of a different species than the raiders, we are under no obligation to use the word “slave.” After all, humans use the labour of a wide variety of species (we “domesticate” them). But observers have also confirmed cases where ants capture individuals of their own species and expropriate their labour power. In any case, non-human animals targeted for

³⁴ “The Migrating Herdsman *Dolichoderus* (*Diabolus*) *Cuspidatus*: An Ant with a Novel Mode of Life,” *Behavioral Ecology and Sociobiology* 17, no. 2 (July 1, 1985): 171–84, <https://doi.org/10.1007/BF00299249>.

³⁵ “Watch Your Language! Racially Loaded Metaphors in Scientific Research,” *BioScience* 57, no. 2 (February 1, 2007): 104–5, <https://doi.org/10.1641/B570203>.

capture and domestication by humans do not host the war system and cannot do organized battle with their captors in a way that we find among ants. For this reason, the parallels with human domestication are not straightforward even when ants raid species other than their own.

It would not be difficult to fashion a definition of slavery that, as in the case of nomadism, would allow the exploration of a system in nature, beyond the bounds of homo sapiens, worthy of comparative study.

War as a system in nature

Returning to war: the remainder of this essay explores aspects of the war system that are revealed in ant wars and human wars. It has three themes: to highlight the remarkable inventiveness of the insect world, to emphasize the many ways that aspects of war we think of as uniquely human have been played out elsewhere in nature over millions of years, and to suggest possibilities for “reciprocal illumination” between the study of these domains.³⁶ We start with one of the archetypal forms of war: territorial wars between nation states.

4. TERRITORY: THE POLITICS OF NATION STATES

As MacMillan observes (above), wars take place between organized societies which “have existed over considerable time, usually in their own territory”. Humans have been fighting wars since we began farming, which produced fixed valuable resources—hence territories—that were worth fighting over, and also sustained communities large enough to mobilize mass, organized, violence.³⁷

Nation states are defined, in part, by their territory, and political scientists seek explanations of war between nation states at three levels: the individual, the societal, and the systemic.³⁸ A neo-realist school sees the behaviour of states as arising from self-interested actions in a world of similar entities jostling for survival in an anarchic (that is, ungoverned) system. These neo-realists “are interested in how structural pressures—as opposed to the

³⁶ Ted Schultz R. et al., “Reciprocal Illumination: A Comparison of Agriculture in Humans and Fungus-Growing Ants,” in *Insect-Fungal Associations: Ecology and Evolution* (Oxford University Press, 2005), 149–90,

<http://www.sbs.utexas.edu/Muelleru/pubs/SchultzEtAl2005RecipIllum.pdf>.

³⁷ Lawrence H. Keeley, *War Before Civilization* (Oxford University Press, USA, 1996).

³⁸ Levy, “The Causes of War and the Conditions of Peace.”

complexities of psychology or domestic politics—shape international outcomes”.³⁹

Ant colonies may be the ultimate neo-realist political unit. Unencumbered by domestic politics or moral considerations, colonies act out of self-interest, with survival as the only metric of success. They have discovered ways to protect their territories from attackers and to expand their territories when the opportunity presents itself.

Weaver ants live in the tree canopies in the “Old World” tropical rainforests of Africa, Asia, Australia, and the Western Pacific.⁴⁰ They build nests by weaving together leaves using larval silk. Their colonies consist of many nests, and may have populations in the millions. Weaver ants are “territorially dominant”: unlike many more selective ant species they feed on many kinds of insect and other prey, and so it makes sense to exclude all competitors from the entire area surrounding and between their nests.⁴¹ Each colony marks out whole trees or large tree limbs as its own territory, and these territories cover the available canopy so densely as to form a “mosaic” of non-overlapping domains,⁴² much as nation state territories fill the map of the world, and each colony defends its own territory against other colonies of their own species and against other competitive species.

Weaver ants mark the edges of their territory with brownish spots containing territorial pheromones unique to each colony,⁴³ and older colony members actively patrol and monitor this boundary, raising the alarm in case of encroachment. As with other animals, weaver ants often fight more aggressively defending their own territory than in attack,⁴⁴ and so the area outside the boundary may become a strip of “no ant land” which other colonies actively avoid. Boundaries may be stable for a number of years, during which time weaver ants exemplify the old human adage “if you want peace, prepare for war”.

³⁹ Anthony C. Lopez and Dominic D.P. Johnson, “The Determinants of War in International Relations,” *Journal of Economic Behavior & Organization* 178 (October 2020): 983–97, <https://doi.org/10.1016/j.jebo.2017.09.010>.

⁴⁰ Berthold K Hölldobler and Edward O Wilson, “Weaver Ants,” *Scientific American*, 1977, 146–54; Bert Hölldobler, “Territoriality in Ants,” *Proceedings of the American Philosophical Society* 123, no. 4 (August 30, 1979): 211–18.

⁴¹ Alain Dejean et al., “Rainforest Canopy Ants: The Implications of Territoriality and Predatory Behavior,” January 1, 2007.

⁴² Dejean et al.

⁴³ B. Hölldobler and E. O. Wilson, “Colony-Specific Territorial Pheromone in the African Weaver Ant *Oecophylla Longinoda* (Latreille),” *Proceedings of the National Academy of Sciences* 74, no. 5 (May 1, 1977): 2072–75, <https://doi.org/10.1073/pnas.74.5.2072>.

⁴⁴ John Maynard Smith, *Evolution and the Theory of Games* (Cambridge: Cambridge University Press, 1982) refers to this as a “bourgeois” strategy.

But weaver ants also show us that this prescription is good only as long as the environment remains stable. Wars break out when the environment receives a shock: when a colony dies, or when a particularly good season leads to population growth. And these wars can be brutal: one colony may take over an entire tree, and may even destroy much or all of the neighbouring colony.

In Central America, the ant "*Pseudomyrmex ferruginea* F. Smith" demonstrates an even more dramatic case of territoriality.⁴⁵ It has developed a symbiotic relationship with a particular species of acacia tree. The tree provides suitable domiciles and a regular supply of food for the ants, while the ants have taken on a strong territorial sense coupled with extreme aggressiveness, and developed an array of weapons to protect their tree. The ants are inseparable from their territory and will attack just about anything that encroaches on it, be it ant, mammal, bird or plant. Colonies fight fiercely with other ant colonies, of the same or different species, for exclusive possession of the tree, and will not hesitate to exterminate their opponents' communities. The colony may rest content with the single tree it has come to regard as its own, but in some cases, it becomes expansionistic, occupying up to 20 trees.

Political scientists treat nation states as acting with intent. They (or their leadership) take decisions, and weigh the costs and benefits of their actions. A "strategy" at the level of a nation state is the result of some form of deliberation. From a game theory perspective, they are assumed to act "rationally". Ant colonies have no such deliberative qualities, no leadership to decide on a strategy, and no hierarchy to implement it. They arrive at their behaviour through millennia of trial and error. That rational decision making and evolution can lead to the same strategic outcomes has been known since Maynard Smith used game theory to understand animal behaviour such as altruism.⁴⁶

Like political scientists, entomologists seek answers at three levels: the individual, the political unit, and the ecosystem to which these units belong. Ant colonies and nation states each act as coherent political units, even if their decision-making mechanisms and social ordering could hardly be more different. Territorial war is not unique to humans: it is a complex phenomenon that has emerged in both human and insect ecosystems, under common pressures and for similar reasons.

⁴⁵ Daniel H. Janzen, "Coevolution of Mutualism Between Ants and Acacias in Central America," *Evolution* 20, no. 3 (1966): 249–75, <https://doi.org/10.2307/2406628>.

⁴⁶ *Evolution and the Theory of Games*.

5. US AND THEM: THE SOCIOLOGY OF IDENTITY

Nation states are more than areas on a map: they must also be politically cohesive if they are to succeed, and this requires a clear sense of who is part of the nation and who is not, particularly in times of war. Discourses of common origin and shared blood relationship are common (terms like "motherland") even when there is no historical or material basis for it. During a war, each side may produce propaganda to emphasize how different "we" are from "them", further deepening the divide.

Individuals face a trade-off between pursuing their individual ends and contributing to the strength of the society of which they are a part. What sociologists call in-group/out-group distinction is associated with increased co-operation among community members in the face of external competition; "conflict with an out-group increases the cohesion of a well-defined in-group".⁴⁷ The "scapegoat hypothesis" or "diversionary theory of war" suggests that leaders may deliberately create or maintain external conflicts to sustain compliance within their state.⁴⁸

The in-group/out-group distinction is also important when it comes to actual combat: effective war-fighting demands that soldiers distinguish "us" from "them", not just by their uniforms, but by how they react to those uniforms. Episodes such as the famous Christmas Truce of 1914, in which soldiers realise their common humanity across the us/them divide, threaten the effective pursuit of war.

The ability to distinguish members of our own group from those who are not, and to make appropriate behavioural adjustments, is widespread in animals. Maintaining the distinction even where very large communities are involved is much rarer. In most primates, for example, animals recognize in-groups by recognizing the individuals that belong to it. In larger societies, individual recognition is not possible; ants share with humans the ability to form what Moffett calls "anonymous societies": individuals recognize members of the same society even if they do not recognize (and may never have met) the individual itself.⁴⁹

For ants, the cue to distinguish members of one colony from another is a complex cuticular hydrocarbon (CHC) profile on the waxy surface of the hard

⁴⁷ H. Kern Reeve and Bert Hölldobler, "The Emergence of a Superorganism through Intergroup Competition," *Proceedings of the National Academy of Sciences* 104, no. 23 (June 5, 2007): 9736–40, <https://doi.org/10.1073/pnas.0703466104>.

⁴⁸ Levy, "The Causes of War and the Conditions of Peace," 152.

⁴⁹ *The Human Swarm: How Our Societies Arise, Thrive, and Fall* (Basic Books, 2019), <https://www.basicbooks.com/titles/mark-w-moffett/the-human-swarm/9781541617292/>.

outer cuticle.⁵⁰ When ants meet, they sense each other's CHC profile through their antennae. The CHC profile is sometimes called an "odour" although the sense involved is somewhere between taste, scent, and touch.

Members of a single-queen, single-nest colony are close genetic relatives. Membership as read by odour matches genetic relatedness and "colony recognition" is the same as "kin recognition". In these cases, the odour acts as a sign to indicate deeper ties, marking who to collaborate with, and who to confront.

But for some ant species, the CHC profile and the "in-group/out-group" distinction has become divorced from relatedness. Many species of wood ant construct extended colonies with multiple nests and queens, in which each ant is only distantly related to others,⁵¹ yet colony group membership is still defined by CHC profile. If nests were isolated, the odour would grow to differ among nests over time, but worker ants move back and forth between nests. Ants exchange odour when they meet through grooming (licking) and trophallaxis (mouth-to-mouth transfer of CHCs),⁵² and in this way the CHC profile is spread among members. There have even been suggestions that worker ants carry brood and other workers between nests to maintain a common odour.⁵³

The CHC profile that a colony maintains this way can be thought of as a "cultural" identity – a distinguishing characteristic that serves not only as a marker of identity but defines it, and which is actively maintained through exchange throughout the members of a colony.⁵⁴ The colony is making a cultural investment in maintaining a common identity among its members: a social infrastructure of cohesion.

An extreme case of ingroup/outgroup recognition among ants is that of the "unicolonial" Argentine ant. A hundred years ago, humans inadvertently transported Argentine ants on ships from their native habitat to new homes where they have become invasive. In these new environments they have

⁵⁰ Candice Torres, M. Brandt, and Neil Tsutsui, "The Role of Cuticular Hydrocarbons as Chemical Cues for Nestmate Recognition in the Invasive Argentine Ant (*Linepithema Humile*)," *Insectes Sociaux* 54 (January 11, 2007): 363–73, <https://doi.org/10.1007/s00040-007-0954-5>.

⁵¹ S. Ellis and E. J. H. Robinson, "Polydomy in Red Wood Ants," *Insectes Sociaux* 61 (2014): 111–22.

⁵² Shelby J Sturgis and Deborah M Gordon, "Nestmate Recognition in Ants (Hymenoptera: Formicidae): A Review," *Myrmecological News* 16 (January 2012): 101–10.

⁵³ Ellis and Robinson, "Polydomy in Red Wood Ants."

⁵⁴ Sara Diana Leonhardt et al., "Ecology and Evolution of Communication in Social Insects," *Cell* 164, no. 6 (March 10, 2016): 1277–87, <https://doi.org/10.1016/j.cell.2016.01.035>.

formed huge multi-nest “supercolonies”, and these colonies have engaged in wars.

The Argentine ant has established supercolonies on several continents. A community discovered in western Europe⁵⁵ stretches 6000 km from northern Italy, through the south of France to the Atlantic coast of Spain—with billions of ants—perhaps even a trillion—occupying millions of nests.⁵⁶

Colony members maintain the ability to identify members of the same colony across continents,⁵⁷ while still identifying outgroup members when neighbouring supercolonies collide.⁵⁸ The largest known ant war on earth is taking place among two Argentine ant colonies in North America. “Each month millions of Argentine ants die along battlefronts that extend for miles around San Diego, where clashes occur with [the “Large Colony” and] three other colonies in wars that may have been going on since the species arrived in the state”.⁵⁹ Researchers observing the conflict concluded that “[O]ver 15 million workers would have died over the six-month period of the study”.⁶⁰ Move a “Large Colony” Argentine ant 800 kilometres from San Francisco to San Diego and she will still be “home”, accepted by surrounding ants. On the other hand, move an ant a few centimetres across an invisible (to humans) border in the outskirts of San Diego, and she will probably be killed by the members of the neighbouring Lake Hodges colony.⁶¹

The anonymous nature of the ingroup/outgroup distinction, so clear in ants, emphasizes that during war the enemy is defined as a group, not as individuals. This anonymity is one feature that makes killing in war different from killing in peacetime. The killing is not personal, it is required by the mass nature of the conflict. At the same time, the individual combatant is disposable from the point of view of the community, entering hostilities with combatants from another colony, at great risk to themselves.

⁵⁵ Tatiana Giraud, Jes S. Pedersen, and Laurent Keller, “Evolution of Supercolonies: The Argentine Ants of Southern Europe,” *Proceedings of the National Academy of Sciences* 99, no. 9 (April 30, 2002): 6075–79, <https://doi.org/10.1073/pnas.092694199>.

⁵⁶ Mark W. Moffett, “Supercolonies of Billions in an Invasive Ant: What Is a Society?,” *Behavioral Ecology* 23, no. 5 (September 1, 2012): 925–33, <https://doi.org/10.1093/beheco/ars043>.

⁵⁷ Ellen Van Wilgenburg, Candice W Torres, and Neil D Tsutsui, “The Global Expansion of a Single Ant Supercolony,” *Evolutionary Applications* 3, no. 2 (March 2010): 136–43, <https://doi.org/10.1111/j.1752-4571.2009.00114.x>.

⁵⁸ Melissa L. Thomas et al., “When Supercolonies Collide: Territorial Aggression in an Invasive and Uniclonal Social Insect,” *Molecular Ecology* 15, no. 14 (November 14, 2006): 4303–15, <https://doi.org/10.1111/j.1365-294X.2006.03038.x>.

⁵⁹ Moffett, “Ants & the Art of War.”

⁶⁰ Thomas et al., “When Supercolonies Collide.”

⁶¹ Moffett, *The Human Swarm: How Our Societies Arise, Thrive, and Fall*, 66–67.

Subtleties in group distinctions

While war and “nestmate recognition” go together, the one does not always lead to the other. Until the 1990s nestmate recognition in ants was thought to be binary: an individual would accept or reject another according to the expression or not of a particular cue.⁶² But as with so much else in the world of ants, the more we learn, the more subtle we discover it to be, and the richer the parallels between ant and human societies become.

As one American observer wrote: “Except when slave-making ants make raids on their neighbours, and when spring competition for extra land causes wars, the ants of the northern states are a peaceful lot. When two ants of different nests meet, the behaviour most frequently observed is the recoil of both ants, and their subsequent pursuit of their peaceful occupations”.⁶³ Forel’s pavement ants and the wood ants of northern Europe, too, typically fight in the spring, after a dormant winter has left boundaries and control over pathways between nests ill-defined, with the wars concluding when boundaries are set.⁶⁴

Like nation states, ant colonies can coexist peacefully for extended periods, but at other times and under the right conditions a small clash may lead to war. Political units invest in maintaining the war system – the capacity to engage in war—but such engagement is still a costly endeavour and it is undertaken only when the pressures require it.

Some species of ant, including the weaver ants discussed above display what is called a “nasty neighbour” effect, whereby ants react more aggressively to neighbours than to strangers.⁶⁵ This behaviour seems to occur most in territorial species with large colony sizes, for which the greatest danger is large neighbouring colonies.

Other ant species develop the opposite: a “dear enemy” effect. They distinguish between the now-familiar neighbours who share the border and non-neighbours (strangers) who have come from further away, and respond *less* aggressively to neighbours than to strangers. This behaviour was observed in *Leptothorax* ants in Europe, which live in small colonies. One

⁶² Sturgis and Gordon, “Nestmate Recognition in Ants (Hymenoptera: Formicidae): A Review.”

⁶³ Laurence J. Lafleur, “Tolerance in Ants,” *The American Naturalist* 76, no. 762 (January 1, 1942): 85–93, <https://doi.org/10.1086/281016>.

⁶⁴ Eldridge S. Adams, “Boundary Disputes in the Territorial Ant *Azteca Trigona*: Effects of Asymmetries in Colony Size,” *Animal Behaviour* 39, no. 2 (February 1, 1990): 321–28, [https://doi.org/10.1016/S0003-3472\(05\)80877-2](https://doi.org/10.1016/S0003-3472(05)80877-2).

⁶⁵ Philip S Newey, Simon K A Robson, and Ross H Crozier, “Weaver Ants *Oecophylla Smaragdina* Encounter Nasty Neighbors Rather than Dear Enemies” 91, no. 8 (2010): 7.

suggestion is that “strangers may have been forced to leave their own nests and might now be searching for a new site, whereas a well-known neighbour typically has its own nest”.⁶⁶

The ability to distinguish “us” from “them” and to respond in ways that are appropriate, seems to be essential to successful political units of large societies.

6. WARRIORS: THE PSYCHOLOGY OF COMBAT

Ants and humans have both, in their own ways, identified techniques for building successful communities in the face of competition from neighbours. Clear boundaries of territory and membership play important roles in limiting unnecessary and accidental outbreaks of war. Still, wars do break out, and when it does, the behaviour of community members changes. Behaviour that is damaging to the community in normal times (killing, aggression) is now necessary.

Human societies have long struggled with the need to develop effective warfighting abilities, while limiting that organized violence to deal with external threats, without overflowing into the daily life of peacetime society. Rituals before going to war, ethical codes for soldiers, heroic myths to emulate all prepare warriors to be ready to kill, and ready to die. They also separate war-time from peace-time norms, with varying degrees of success.

Ant societies face the same challenges. Mustering a collective response to a threat demands the rapid raising of an alarm, alerting others to the presence of an enemy. It must assemble nestmate responders and set in motion a change in their behaviour, so that they are disposed to aggression.

“Recruitment” is the term for communication bringing nestmates to a location where activity is required. Colony members recruit others for a range of activities, a prominent one being response to threats such as floods, attacks by large animals (bears, anteaters), or attacks by other ants. Recruitment in

⁶⁶ Charlotte Christensen and Andrew N. Radford, “Dear Enemies or Nasty Neighbors? Causes and Consequences of Variation in the Responses of Group-Living Species to Territorial Intrusions | Behavioral Ecology | Oxford Academic,” *Behavioural Ecology* 29, no. 5 (October 2018): 1004–13; Jürgen Heinze et al., “Apparent Dear-Enemy Phenomenon and Environment-Based Recognition Cues in the Ant *Leptothorax Nylander*,” *Ethology* 102, no. 3 (1996): 510–22, <https://doi.org/10.1111/j.1439-0310.1996.tb01143.x>; T. A. Langen, Frédéric Tripet, and Peter Nonacs, “The Red and the Black: Habituation and the Dear-Enemy Phenomenon in Two Desert Pheidole Ants,” *Behavioral Ecology and Sociobiology* 48, no. 4 (September 1, 2000): 285–92, <https://doi.org/10.1007/s002650000223>; MC Pereira et al., “Dear Enemy Phenomenon in the Ant *Ectatomma Brunneum* (Formicidae: Ectatomminae);” 2019, 9.

the face of threat must be fast, and some species of ants respond so quickly to a flooding domicile that “one or two workers can mobilize a large fraction of the colony in 30 seconds or less and even initiate colony immigration”.⁶⁷

Recruitment typically involves chemical signals and mechanical gestures. It is more complex than a simple cry of “alarm!”: faced with combat, a weaver ant uses a short-range recruitment pheromone to summon immediate reinforcements, but also returns to the nest, depositing a different pheromone to mark a trail back to the site of conflict, and “jerks its body at passing ants to alert them to the ongoing combat”. Weaver ants may use different pheromones when recruiting for other purposes, such as to occupy a previously unoccupied space for the nest.⁶⁸

The “decision” to recruit also has subtleties. We have already seen that wars among wood ants break out only at times of the year when nutrition is scarce. Ants may also behave differently depending on whether the queen is nearby,⁶⁹ and some fighting ants can assess group sizes, recruiting nestmates only when they outnumber opponents.⁷⁰

Once mobilized, risk-taking and self-sacrifice are common in warfare, in ants as in humans. Students of formic behaviour have referred to this as evidence of “extreme altruism.” A remarkable example is the “suicide warriors” of *Camponotus*.

*Two huge glands, filled with toxic secretions, run from the bases of the mandibles all the way to the posterior tip of the body. When the ants are pressed hard during combat...they contract their abdominal muscles violently, bursting open the body wall and spraying the secretions onto the foe.*⁷¹

The flight from psychology

While there are commonalities between the study of humans and ants at the system level (neo-realism) and at the societal level (in-group/out-group distinctions), the differences in how we think about the two are stark at the level of the individual organism.

⁶⁷ Hölldobler and Wilson, *The Ants*, 171.

⁶⁸ Moffett, “Ants & the Art of War.”

⁶⁹ Sturgis and Gordon, “Nestmate Recognition in Ants (Hymenoptera: Formicidae): A Review.”

⁷⁰ Eldridge S. Adams and Nicola J.R. Plowes, “Self-Organizing Conflicts: Group Assessment and the Spatio-Temporal Dynamics of Ant Territory Battles,” *Behavioural Processes* 162 (May 2019): 119–29, <https://doi.org/10.1016/j.beproc.2019.01.009>.

⁷¹ Hölldobler and Wilson, *Journey to the Ants: A Story of Scientific Exploration*, 67.

The experiences of individual soldiers in human wars have been mythologized, studied, and told in stories down the centuries. There is a rich tapestry of heroism, comradeship, fear, confusion, bravery, discipline, cowardice, compulsion and much more arising from the extremity of facing and dealing death. Societies draw on religion, ritual, drugs and discipline to manage and contain the forces of war.

In contrast, essentially nothing is told of the experiences of ants. Do they have experiences at all? Here the practice of entomologists borrowing terminology from human wars comes to a halt. The contrast is dramatic. Self-sacrifice in wartime is seen, when carried out by humans, as an expression of bravery and nobility sufficient to prompt some of our most universal and challenging stories of what it means to be human. The same action carried out by ants is simply “stereotyped behaviour” with no implications of “intent” or internal states. The use of the words “alarm” and “excite”, both of which can also be applied to inanimate objects, is as close as most studies go.

We confess that it is not always easy, at least for those of us who are not ant specialists, to see where the stereotyped behaviour ends and intelligent decision-making begins. We are told, for example, that “one fire-ant worker straggling close by is enough to trigger a violent response” in the woodland ant.⁷² Here are found, presumably, both the cue and the stereotyped behaviour, but the behaviour evoked may be quite complex. The worker ant, having encountered the fire-ant and identified it, (i) touches it to acquire its odour; (ii) lays down a chemical trail; (iii) rushes up to nestmates one at a time as she hurries back to the nest. Then, as part of this same sequence of actions, both “soldiers” (majors) and ordinary workers quickly attack the enemy and kill it, after which they search the area for further members of the fire-ant nest. This may end the matter, but in some cases a wider engagement may take place. We confess that it is not clear to us where the stereotyped phase ends and a phase of intelligent action begins.

Early entomologists did not all share this outlook. August Forel, describing the fighting state of Amazon ants, said: “the battle-fury sometimes becomes terrible; they snap right and left with their jaws and abandon all distinction between friend and foe. They are like mad creatures.” Forel was implying the existence of a particular psychological state. He interpreted what he saw in terms of human war: “battle-fury” reminds us of Viking Berserkers, and is a theme well known in the literature of human war.

⁷² Hölldobler and Wilson, 60.

We wonder, when all is said and done, whether the flight from psychology can be justified or is simply a path of least resistance for the natural sciences. We are not convinced that there are good reasons to deny or ignore the existence of psychological states in ants or to rule out all possible human knowledge of them. Such questions have been faced before in the study of other species and the positivist view has not always emerged intact. Most notably, the early challenges faced by Jane Goodall to have her observations and interpretations taken seriously by primatologists show that such questions are not closed.

We are sympathetic to Wheeler's treatment of the issue in his famous 1910 one-volume treatment of the ants:

"The question then suggests itself as to whether there is anything to indicate that ants experience similar internal states. We are, of course, working here merely with analogical inferences and probabilities, and may, therefore, incur the contempt of a whole school of German physiologists, but, as has been often stated by other authors, we must either proceed in this manner or abandon animal psychology altogether. I admit that it is very easy and very reprehensible to read one's own psychology into an animal, but after a patient, and, I believe, unprejudiced study of the ants, I have reached the same conclusions as Forel, Wasmann and others, namely, that these insects show unequivocal signs of possessing both feelings and impulses."⁷³

Wheeler was Professor of Applied Biology at Harvard University and one of the world's most respected students of ants when he wrote this passage.⁷⁴

Try as they might, entomologists cannot entirely escape interpretation. By avoiding any mention of intent or of internal states, researchers implicitly treat ants as information-processing and algorithm-following automata, a stance that blends smoothly into agent-based computer simulations of ant behaviour.⁷⁵ Yet ants are not interchangeable; they are individuals, with memories of their own unique life histories. They memorize complex foraging routes for periods of weeks, distinguish among complex pheromone profiles

⁷³ Wheeler, *Ants: Their Structure, Development, and Behavior*, 529.

⁷⁴ "Wheeler, William Morton (1865-1937) - AntWiki," accessed January 31, 2021, [https://www.antwiki.org/wiki/Wheeler,_William_Morton_\(1865-1937\)](https://www.antwiki.org/wiki/Wheeler,_William_Morton_(1865-1937)).

⁷⁵ Kit Martin and Pratim Sengupta, "Multi-Agent Simulations of Intra-Colony Violence in Ants" (Springer, 2020), <https://prism.ucalgary.ca/handle/1880/112121>.

(see above), and undertake sequences of context-dependent decisions. A forest-dwelling African *ponerine* ant “memorizes the detailed outline of tree crowns beneath which it passes on outgoing trips, then integrates and reverses the information upon its return to run a straight line home”.⁷⁶

Current trends in modern war fighting may be heading in the opposite direction, turning human soldiers into information-processing manageable units. Chemical-induced behaviour changes have long been common in human warriors of course, from Dutch courage to ritual consumption of intoxicants to today’s medically-tuned performance enhancers. Technological innovations continue to replace or control human soldiers by computer-assisted decision-making, policy-implementing workflows, or automated weaponry, all seeking to render redundant the psychology of the battlefield.

7. THE MILITARIZED STATE

Despite war’s comparative rarity, it has often precipitated long-lasting changes in the organization of societies. The demands of war require the state to take a central role, and that role has not been given up with the end of conflict.

In ants, war is one of the forces driving the formation of new “castes”. Among ants, function is often connected to physical type or state and the term “caste” has been used for a long time, for better or worse, to express this convergence. “A caste is any set of a particular morphological type, age group, or physiological state (such as inseminated versus barren) that performs specialized labour in the colony”.⁷⁷

Among the workers, who are all female, the most common morphological types are minor, media and major, which have differing body size and other specialized physical attributes. The difference in size between minor and major nestmates reaches an apex in marauder ants, where the major ants may weigh five hundred times more than a minor, and where the minor may ride on the head of the major.⁷⁸

War is “a strong and recurrent pressure” driving the development of distinct castes in a species, “including the evolution of a functionally

⁷⁶ Hölldobler and Wilson, *The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies*, 118.

⁷⁷ Hölldobler and Wilson, *The Ants*, 300, or 360.

⁷⁸ Moffett, “Ants & the Art of War.”

specialized and large soldier caste”.⁷⁹ As an aside: The nature of division of labour is still controversial. Deborah Gordon argues that “‘Division of labour’ is a misleading way to describe the organization of tasks in social insect colonies, because there is little evidence for persistent individual specialization in task.”⁸⁰ Robert Jeanne responds that “Division of labour is not a process or a misleading concept”.⁸¹ Either way, the topic is lively.⁸²

Consider three ant species of the genus *Camponotus*, which live in the southern United States and are subject to predatory raids by army ants. One of those species responds to raids by flight, evacuating the nest and carrying their brood with them. The other two species respond by fighting, with the majors taking a leading role. All three species have “major” and “minor” castes, but in the one that flees the majors are only slightly larger than the minors. In those that fight, the majors are much larger. The researchers conclude that the army ant raids are sufficient to produce this specialization.⁸³

Across humans and ants, war has driven changes in society to enable it to put all its weight behind the achievement of a single goal, demanding increasingly specialized roles and communication techniques, and changing the relationship among members of society. One has achieved this goal through a centralized state and the other through decentralized coordination.

Lanchester's laws and military investment

Nothing is simple when it comes to ants: warfare does not *always* drive specialisation. Leafcutter ants and others may have developed multiple castes with complex functions in part as a response to wars, but other ants remain unspecialised. The Argentine ants engaged in massive wars in California and New Mexico (above) have just a single worker caste, as do the wood ants of Europe. Why this difference?

⁷⁹ Bill D. Wills et al., “Correlates and Consequences of Worker Polymorphism in Ants,” *Annual Review of Entomology* 63, no. 1 (January 7, 2018): 575–98, <https://doi.org/10.1146/annurev-ento-020117-043357>.

⁸⁰ Deborah M. Gordon, “From Division of Labor to the Collective Behavior of Social Insects,” *Behavioral Ecology and Sociobiology* 70, no. 7 (July 1, 2016): 1101–8, <https://doi.org/10.1007/s00265-015-2045-3>.

⁸¹ Robert L. Jeanne, “Division of Labor Is Not a Process or a Misleading Concept,” *Behavioral Ecology and Sociobiology* 70, no. 7 (July 1, 2016): 1109–12, <https://doi.org/10.1007/s00265-016-2146-7>.

⁸² Theo C. M. Bakker, “Editorial: Special Issue on Integrative Analysis of Division of Labor,” *Behavioral Ecology and Sociobiology* 70, no. 7 (July 1, 2016): 993–94, <https://doi.org/10.1007/s00265-016-2132-0>.

⁸³ Brent Lamon and Howard Topoff, “Avoiding Predation by Army Ants: Defensive Behaviours of Three Ant Species of the Genus *Camponotus*,” *Animal Behaviour* 29, no. 4 (November 1, 1981): 1070–81, [https://doi.org/10.1016/S0003-3472\(81\)80060-7](https://doi.org/10.1016/S0003-3472(81)80060-7).

The explanation can be found in one of the more successful applications of “human war” studies to the insect world, initially by Franks and Partridge.⁸⁴ “Lanchester’s laws of conflict”, developed during World War 1, loosely state that in open environments where individuals can gang up on enemies, the army with the *most* combatants is likely to win (this is also called the “square law”). In confined spaces and other environments where one-on-one combat is more likely, the army with the *best* combatants wins (the “linear law”).

When the “square law” applies, the quality of the soldiers is unimportant. A society that faces predominantly “square law” warfare will not invest in producing a skilled army, so long as it can muster large numbers of cheap soldiers when it needs them. “Before the advent of modern war... European powers preferred to use the most expendable members of society to fill up the ranks of their armies”⁸⁵. In wars between wood ant colonies, which may lead to thousands of deaths per day, “the warriors are workers from the oldest generation... The toll taken by war thus concerns individuals who would have died anyway”.⁸⁶

Even societies that do have specialised armies may be selective when to deploy their elite troops. War has produced new forms of organization among ants: the development of military tactics. “In the foraging arena, the evolution of body-size variation can provide both a numerous worker caste for combat in open areas and larger, more capable fighters for spatially constrained combat scenarios... the small, fast workers of *Pheidole* species can be critical in locating and numerically dominating rich food resources, and then soldiers defend the resources against subsequent usurpation attempts by competitors”.⁸⁷

Army ant and marauder ant colonies have multiple castes, but their raids draw on massive numbers of the tiny and disposable “minor” workers, which take their place at the front lines. The much larger “soldier” castes are protected, and fight more selectively.

Leafcutter ants also have a “true soldier caste” of very large majors with sharp mandibles, which respond when a nest of is attacked by vertebrates.⁸⁸ When threatened by other ants the combat is usually out in the open, the

⁸⁴ “Lanchester Battles and the Evolution of Combat in Ants,” *Animal Behaviour* 45, no. 1 (1993): 197–99, <https://doi.org/10.1006/ANBE.1993.1021>.

⁸⁵ MacMillan, *War*, 125.

⁸⁶ A. Mabelis, “Aggression in Wood Ants (Formica Polycytena Foerst., Hymenoptera, Formicidae),” *Aggressive Behavior* 10, no. 1 (1984): 47–53, [https://doi.org/10.1002/1098-2337\(1984\)10:1<47::AID-AB2480100107>3.0.CO;2-N](https://doi.org/10.1002/1098-2337(1984)10:1<47::AID-AB2480100107>3.0.CO;2-N).

⁸⁷ Wills et al., “Correlates and Consequences of Worker Polymorphism in Ants.”

⁸⁸ Hölldobler and Wilson, *The Leafcutter Ants: Civilization by Instinct*, 58.

Lanchester square law applies, and the colony sends large numbers of smaller workers to war.⁸⁹ But there is yet another exception: when attacked by subterranean army ant colonies seeking to plunder the leafcutter brood as food, soldiers barricade nest entrances where they can engage in one-on-one combat.⁹⁰

The American army invests heavily in each soldier, and in Afghanistan it has faced an opponent with few resources. Bellany argues that the Americans must fight in ways that the “linear law” applies.⁹¹ The conclusion is not obvious: “If you have more effective weapons than your opponent, Lanchester says you must engage the enemy less closely if you want the advantage to really tell.” You must fight from a distance, protecting your own expensive soldiers, even if this approach leads to the killing of enemy civilians.

The costs of maintaining an army

Maintaining a war system between outbreaks of conflict incurs substantial costs, without immediate benefits.

Hölldobler and Wilson remark that soldier ants in many species spend a fair bit of their time doing nothing, “rather like fully fuelled interceptor jets on a carrier deck.”⁹² Some soldier ants are so specialized that they cannot feed themselves and must be fed by workers. She is a drain on the resources of the colony during these times. But she cannot shed her role, which is in-built—is inscribed in her body and mind—and is a living sign of the war system even when this system is in its cold state.

Ants and humans have each discovered that the cost of maintaining an army can be more easily afforded if it is used for other purposes apart from war. Some ant “soldiers” perform tasks such as crushing seeds,⁹³ and also exert themselves violently against many different species, and some of these actions are not part of war as defined in this article. For instance, leafcutter “soldiers” defend their colony against members of different taxonomic classes, such as *Mammalia* and *Aves*. Is the term “soldier” still applicable?

⁸⁹ Mary E. A. Whitehouse and Klaus Jaffe, “Ant Wars: Combat Strategies, Territory and Nest Defence in the Leaf-Cutting Ant *Atta Laevigata*,” *Animal Behaviour* 51, no. 6 (June 1, 1996): 1207–17, <https://doi.org/10.1006/anbe.1996.0126>.

⁹⁰ Scott Powell and E. Clark, “Combat between Large Derived Societies: A Subterranean Army Ant Established as a Predator of Mature Leaf-Cutting Ant Colonies,” *Insectes Sociaux* 51 (January 11, 2004): 342–51, <https://doi.org/10.1007/s00040-004-0752-2>.

⁹¹ “Fighting Asymmetric Wars: An Application of Lanchester’s Square-law to Modern Warfare,” *The RUSI Journal* 147, no. 5 (October 1, 2002): 72–76, <https://doi.org/10.1080/03071840208446819>.

⁹² Hölldobler and Wilson, *Journey to the Ants: A Story of Scientific Exploration*, 60.

⁹³ Wheeler, *Ants: Their Structure, Development, and Behavior*, 98.

Modern human soldiers also carry out many functions other than fighting wars. When emergencies demand a large-scale coordinated response, many countries call in the army. Responding to floods, distributing vaccine during pandemics, fighting off anteaters: a specialized caste of soldiers takes a multifaceted role in society, with a particular focus on emergencies.

Some ants appear to have outsourced the cost of defence to mercenaries. *Sericomyrmex* is a fungus-growing species, and the genus *Megalomyrmex* has made its home in *Sericomyrmex* nests, an action that would seem to be parasitic. But *Sericomyrmex* nests are also the target of attack by “agro-predator” species, and the guest ants protect their host colonies using a potent venom that is much more effective than the biting defences of the host ants.⁹⁴

Another lesson about the war system is revealed in the soldier ant. The inscription of war in her body and mind implies the presence of the system in other formic communities as well. All the communities and species that host war participate in the system, and the system becomes visible in the multiple interactions of these communities and species. The soldier ant in a particular colony needs her mandibles and her aggressiveness because of the existence of warlike ants elsewhere, and *vice versa*. Each implies and requires the other. The same is true of war among human beings: If I need to be warlike it is because you are, and vice versa.

8. TECHNOLOGY AND INNOVATION

The militarized state is the organization of society so as to be able to fight wars effectively. But innovation is not limited to social organization: there is also a long history of war-driven technological innovations in both ants and humans, most obviously in the development of more lethal weapons and more effective defences.

Ants have not only developed a distinct soldier “caste” in some species, but have also equipped them with specialized weaponry, designed to be effective against specific groups of foes. Science journalist Erich Hoyt⁹⁵ wrote about formic war in his book, *The Earth Dwellers*, and he distinguishes “mandibular techniques” from “chemical warfare.” Under the first category (see p. 206) he says:

⁹⁴ Rachele M. M. Adams et al., “Chemically Armed Mercenary Ants Protect Fungus-Farming Societies,” *Proceedings of the National Academy of Sciences* 110, no. 39 (September 24, 2013): 15752–57, <https://doi.org/10.1073/pnas.1311654110>.

⁹⁵ *The Earth Dwellers: Adventures in the Land of Ants*, Reprint edition (New York: Simon & Schuster, 1997).

"Hatchet-shaped mandibles can slice through the chitinous exoskeleton or chop off the legs of an opponent." (Examples include many Pheidole species as well as leaf cutters.) "Saber- or hook-shaped mandibles with pointed tips that turn in at the end." "When an enemy ant gets its head or body caught inside these jaws, the result is instant death." (Examples include various of the "swarm-raiding and column-raiding army ants, and some of the notorious slave-making species.") "Trap mandibles, as used by the dacetine tribe and some of the ponerines, consist of elongated mandibles that snap shut convulsively, impaling prey or enemies on the sharp teeth at or near the tip."

Hoyt notes that "almost all ants use some chemical warfare," the weapons of which he distinguishes as "stings, sprays and secretions."

The sting is one of the defining features of ants, and is particularly effective against threatening vertebrates. As ants became more abundant, their greatest threat shifted from vertebrates to other ants and some species lost their sting, or modified it into a "chemical weapons delivery system", enhancing their ability "to attack and fight off and win battles against other ants".⁹⁶

We have already seen the "kamikaze" weapons of *Camponotus* ants, but chemical weapons can also be used for defence. In northern California the native winter ant has been able to preserve itself against the Argentine ant while other species have succumbed; its success is partly thanks to a secretion they apply directly to the body of their invasive foe, killing it within an hour, four times out of five.⁹⁷

Technological innovation is not limited to weapons. Leafcutter ant soldiers have developed a biomineral armour overlaying their exoskeleton which provides additional protection in battles and against disease.⁹⁸ The 119 different species of turtle ants have been known as "an iconic example of caste specialization" since Darwin. Turtle ants make their homes in pre-existing cavities⁹⁹ and when the nest is threatened the elaborately armoured heads of

⁹⁶ Sean O'Donnell, "Ant Wars," *Serious Science* (blog), August 25, 2016, <http://serious-science.org/ant-wars-6652>.

⁹⁷ Trevor R. Sorrells et al., "Chemical Defense by the Native Winter Ant (*Prenolepis Imparis*) against the Invasive Argentine Ant (*Linepithema Humile*)," *PLOS ONE* 6, no. 4 (April 19, 2011): e18717, <https://doi.org/10.1371/journal.pone.0018717>.

⁹⁸ Hongjie Li et al., "Biomineral Armor in Leaf-Cutter Ants," *Nature Communications* 11, no. 1 (November 24, 2020): 5792, <https://doi.org/10.1038/s41467-020-19566-3>.

⁹⁹ Scott Powell, "A Comparative Perspective on the Ecology of Morphological Diversification in Complex Societies: Nesting Ecology and Soldier Evolution in the Turtle Ants," *Behavioral*

their soldier caste act as living barricades. Some cavities have entrances much larger than the head of one soldier and among the species that live there, soldier heads are square or dome-shaped and several soldiers will cooperate to block the entrance. In contrast, for species that live in cavities with smaller entrances, a single soldier will block it by locking its disc or dish-shaped head into place.¹⁰⁰

Technologies of deceit

Slave-making ants are “constrained by their life style to be outnumbered by workers in the colonies they fight” and Lanchester’s laws suggest this arrangement creates a space for technological innovation.¹⁰¹ These species have responded by developing techniques of deceit.

One technique is the use of “propaganda substances”.¹⁰² Invading ants broadcast pheromones that mimic an alarm signal of the host species. This induces panic in the attacked ants, dispersing them and weakening their ability to resist the invaders.

Like human propaganda but different to most of the weapons we have met so far, this is a weapon that acts on a whole population. It may not be “mass destruction”, but perhaps it is “mass deception”, allowing the raiders to avoid fighting with those whose colony they invade.

Slave-making ants also employ chemicals that override the most crucial of formic abilities, the ability to recognize each other as members of the same society. Instead, members of host nest attack each other as if they were facing alien invaders.¹⁰³

To return to the question of psychology: should the term “deception” be used in dealing with *formicidae*? Do we need to know the details of ants’

Ecology and Sociobiology 70, no. 7 (July 1, 2016): 1075–85,
<https://doi.org/10.1007/s00265-016-2080-8>.

¹⁰⁰ Scott Powell, Shauna L. Price, and Daniel J. C. Kronauer, “Trait Evolution Is Reversible, Repeatable, and Decoupled in the Soldier Caste of Turtle Ants,” *Proceedings of the National Academy of Sciences* 117, no. 12 (March 24, 2020): 6608–15,
<https://doi.org/10.1073/pnas.1913750117>.

¹⁰¹ Franks and Partridge, “Lanchester Battles and the Evolution of Combat in Ants.”

¹⁰² F. E. Regnier and E. O. Wilson, “Chemical Communication and ‘Propaganda’ in Slave-Maker Ants,” *Science* 172, no. 3980 (April 16, 1971): 267–69,
<https://doi.org/10.1126/science.172.3980.267>.

¹⁰³ Anthony B. Allies, Andrew F. G. Bourke, and Nigel R. Franks, “Propaganda Substances in the Cuckoo Ant *Leptothorax Kutteri* and the Slave-Maker *Harpagoxenus Sublaevis*,” *Journal of Chemical Ecology* 12, no. 6 (June 1, 1986): 1285–93, <https://doi.org/10.1007/BF01012348>;
M. Brandt et al., “Convergent Evolution of the Dufour’s Gland Secretion as a Propaganda Substance in the Slave-Making Ant Genera *Protomognathus* and *Harpagoxenus*,” *Insectes Sociaux* 53 (August 1, 2006): 291–99, <https://doi.org/10.1007/s00040-006-0871-z>.

cognitive states? If we cannot know about such states, can we say that they are deceived? We note simply that many myrmecologists, even when they do not raise the question directly, appear to accept deception among ants as fact, as when Wilson and Hölldobler say: “ants employ propaganda, deception.”¹⁰⁴ During the discussion of parasitism, they routinely imply that certain kinds of parasites are successful in surviving in ant communities because they are able to fool the ants.

There are other, similar cases. Consider a species of ants whose members are able to make their way, without being stopped and killed, into an ant domicile of a different species, even entering the chamber where the queen is located. These infiltrators then kill the queen, replace her with one of their own, and manipulate host workers to direct their altruistic behaviours towards the parasites rather than their own relatives.¹⁰⁵ Discussions of such cases by myrmecologists appear to take it for granted that the ants of the violated domicile are deceived.

9. LIMITED WAR AND ETHICS

War is a costly enterprise, even for the victor, who may be left weakened by the extremities of combat. Humans throughout history have searched for ways to avoid war where possible, and to limit the devastation of war by devising rules for its conduct. Yet MacMillan quotes Pancho Villa as saying “limiting war is a silly idea: war is not a game”. From a different perspective, White House Counsel Alberto Gonzalez was quoted as saying that in the War on Terror, the Geneva Conventions are “quaint”.

Is the search for ways to limit war a pipe dream? Here, ants may offer signs of hope: they have found ways to limit the frequency and intensity of their wars, and nobody could accuse them of being quaint or silly.

Negotiations and intelligence gathering

We have already seen that establishing clear borders, patrolling them and marking them, may serve to establish long periods of peace between ant colonies. Still, there are times when ecosystem pressures bring conflict to the surface. At such times, intelligence gathering can help to avoid or limit open warfare. If the relative strength of two political units can be established, perhaps an agreement can be made with the same end result, but with each

¹⁰⁴ Hölldobler and Wilson, *The Ants*, 461.

¹⁰⁵ P. D’Ettorre and J. Heinze, “Sociobiology of Slave-Making Ants,” *Acta Ethologica* 3, no. 2 (April 23, 2001): 67–82, <https://doi.org/10.1007/s102110100038>.

side avoiding the cost of open warfare. In humans this is the sphere of diplomacy and negotiation.

Honey pot ants may not sit down at tables, but they do engage in ritual encounters with a view to avoiding open war. They stage “tournaments”, amassing large numbers of workers from opposing colonies, which then square off in contested zones and stage numerous one-on-one confrontations between members of the two colonies.¹⁰⁶ These appear to be dominance contests, with posturing and pushing but little or no serious fighting. (“The ants challenge one another back and forth across the disputed field in the manner of medieval knights, one on one.”¹⁰⁷) Sometimes the contests go on for quite a while and result in the attainment of stable borders between the two colonies.

It has been argued that one of the functions of these contests is the assessment of the size and strength of the opposing colony. If one colony concludes that it has superiority in numbers at a scale of ten to one or more, it will often invade and destroy the weaker colony.^{108,109}

The tawny crazy ant (*Nylanderia fulva*) is another example of limited war fighting: “intraspecific aggression between ants from different nests is common and ritualized. Aggression is typically one-sided and follows a stereotyped sequence of escalating behaviors that stops before actual fighting occurs”.¹¹⁰

Meat ants live in single nests near eucalyptus trees in Australia, and each nest is the focus of a well-defined network of trails and foraging sites that define a stable territory. When meat ants encounter ants from other colonies, they raise their gasters and “posture aggressively”. These ritualized displays resolve boundary disputes and clarify each colony’s territory. The authors offer an alternative interpretation that is even more like a negotiation: they suggest that the display is not so much an aggressive display as a solicitation of food. The ant raising its body demands food from the other, trying to get the

¹⁰⁶ Hölldobler, “Tournaments and Slavery in a Desert Ant.”

¹⁰⁷ Hölldobler and Wilson, *Journey to the Ants: A Story of Scientific Exploration*, 69–70.

¹⁰⁸ Hölldobler and Wilson, 73.

¹⁰⁹ Hölldobler, “Tournaments and Slavery in a Desert Ant”; Hölldobler, “Territoriality in Ants”; Hölldobler and Wilson, *The Ants*, 406ff; Hölldobler and Wilson, *Journey to the Ants: A Story of Scientific Exploration*, 69ff; E. van Lieshout, M. A. Elgar, and E. van Wilgenburg, “Conflict Resolution Strategies in Meat Ants (*Iridomyrmex Purpureus*): Ritualised Displays versus Lethal Fighting,” *Behaviour* 142, no. 6 (January 1, 2005): 701–16, <https://doi.org/10.1163/1568539054729150>.

¹¹⁰ Edward G. LeBrun et al., “Ritualized Aggressive Behavior Reveals Distinct Social Structures in Native and Introduced Range Tawny Crazy Ants,” *PLOS ONE* 14, no. 11 (November 22, 2019): e0225597, <https://doi.org/10.1371/journal.pone.0225597>.

other to fold its mandibles and submit. The loser lowering its body resembles the attitude adopted by a donor in feeding.¹¹¹ Whatever the interpretation, the display often resolves border disputes in a non-violent manner.

Combination and colonization

The “polydomous” and “polygynous” communities discussed in “Us and them: the sociology” above show another approach to avoiding war: individual nests accept traffic and exchange, so avoiding the cost of war and combining their efforts in an arrangement that, in some conditions, is more successful, with the “unicolonial” ants as the most dramatic example.

Ideas about “just war” extend also to the treatment of the losing state. It is true that in some cases, the treatment by ants is to eat their enemies, but in other cases they are more generous. When colonies of an African acacia ant engage in territorial wars, even the victorious colony may suffer significant fatalities, leaving it potentially vulnerable to predators. Once a queen is killed, “former enemies coexist with victorious colony members in shared nests”, and so the citizens of the losing colony contribute to the strength of the victorious one.¹¹²

Colonization also occurs in *myrmicine* ants in Europe which live in small colonies in rotting branches and similar sites. “Nest sites become scarce in summer due to rapid decay, and both established colonies and young founding queens face a severe shortage of suitable nest sites. This leads to the fusion of established, unrelated colonies, which after initial fighting permanently merge and live together. Typically only one queen survives after fusion.”¹¹³

From limited war to ethics

Ants may not engage in moral assessments of “just war”, yet we can still learn lessons from them about the possibilities for limited war and means to avoid war.

¹¹¹ G. Ettershank and J. A. Ettershank, “Ritualised Fighting in the Meat Ant *Iridomyrmex Purpureus* (Smith) (Hymenoptera: Formicidae),” *Australian Journal of Entomology* 21, no. 2 (1982): 97–102, <https://doi.org/10.1111/j.1440-6055.1982.tb01772.x>.

¹¹² Kathleen P. Rudolph and Jay P. McEntee, “Spoils of War and Peace: Enemy Adoption and Queen-Right Colony Fusion Follow Costly Intraspecific Conflict in Acacia Ants,” *Behavioral Ecology* 27, no. 3 (January 1, 2016): 793–802, <https://doi.org/10.1093/beheco/arv219>.

¹¹³ Moffett *The Human Swarm: How Our Societies Arise, Thrive, and Fall*, 288. asserts that “In dispatching the spoils of war, across all ant species there are only two options: to take slaves or to wipe out the losers, in which case cannibalism is common”. The merging of nests seems to contradict this assertion.

At the most general level (why do wars happen at all?), a strand of thought seeks the ultimate causes of war in human nature. As MacMillan writes: “certain motives appear again and again: greed, self-defence, and emotions and ideas” (p 35). Elsewhere, she writes that “Wars usually start for one of three reasons: greed, fear and ideology”.¹¹⁴ Ants show us that, while human nature is consistent with war, it is not required.

The ideas that war should be pursued according to a mutually agreed on set of implicit or explicit rules, has evolved most commonly between culturally similar warring enemies, who may share a set of values and see each other as truly human.¹¹⁵ Agreement to a set of conventions or limits can be seen as mutually beneficial in the long run, but in the case of a single war the short-term incentive is to violate the conventions if need be. Ant wars among colonies of the same species tend to repeat themselves millennium after millennium, and any strategy that trades long-term pain for short-term gain may not last. Just as the equilibrium to a single-round prisoner’s dilemma is to defect, but co-operation can be sustained through repeated play, so the repeated wars among ants may select for limited war-making. From an ethical point of view, while ants may not engage in moral assessments, there are reasons why they may be good consequentialists.

10. ASYMMETRIC AND UNILATERAL VIOLENCE

Both ants and humans take part in raids and invasions to plunder the resources of other communities. Here we focus on the case where the “resources” to be acquired are the inhabitants themselves (often taken in the brood stage), to be used as either food or labour by the invading colony. The killing of other animals as food is called predation; the acquisition of other ants for use as labour is called slavery. Both have been identified as distinct systems with their own dynamics, but both overlap with war.

We have already met examples of each. For both there is a spectrum of mutuality: to the extent the targets fight back in an organized manner, we may call these events “wars”, but there are also cases where the target does not fight back. In such cases, mass, organized lethal violence may be carried out by one political unit against another, but it will not be mutual.

¹¹⁴ MacMillan, *War*.

¹¹⁵ Alexander Moseley, “The Philosophy of War,” in *Internet Encyclopedia of Philosophy*, accessed February 21, 2021, <https://iep.utm.edu/war/>.

Predation

“Army ants” is the term used to describe species that do not maintain a static nest, but travel in search of food: a colony of hundreds of thousands continuously on the move, highly organized and hunting as a unit^{116, 117} *Nomamyrmex esenbeckii* is a species of army ant that lives primarily underground, or at least under leaves and sticks, and feeds on the eggs and larvae (brood) of a variety of other insects.¹¹⁸ Colonies of this ant will launch raids on young and also mature leafcutter ant colonies, and the leafcutter ants fight back. The outcome of these raids varies: leafcutter ants succeed in repelling some raids, other raids succeed in stealing kilograms of brood. In some cases, the army ants destroy the entire leafcutter colony.

War and predation overlap, dramatically in some species. In weaver ants there is “a lack of any clear distinction on the part of the workers between colony defence and predation. When defenders vanquish invading ants, they remove them to the nest interior and convert them into food”.¹¹⁹

A similar overlap has been seen among the wood ants of The Hague, but here the prey / enemy are of the same species as their predators. Mabelis has suggested that the main function of war among wood ants may be to acquire food, in the form of other wood ants, for queens and males.¹²⁰ This extra nutrition may bring forward the mating flight dates of the queens and improve the chance of propagating their genes.

The overlap between predation and war shows in other ways. Hölldobler and Wilson note that “many species employ a single alarm-recruitment procedure to alert nestmates to both enemies and prey, and in fact the distinction between the two may be wholly blurred with reference to communication”.¹²¹

¹¹⁶ Theodore Christian Schneirla and T. C. Schneirla, *Army Ants: A Study in Social Organization* (W. H. Freeman, 1971); S. G. Brady, “Evolution of the Army Ant Syndrome: The Origin and Long-Term Evolutionary Stasis of a Complex of Behavioral and Reproductive Adaptations,” *Proceedings of the National Academy of Sciences* 100, no. 11 (May 27, 2003): 6575–79, <https://doi.org/10.1073/pnas.1137809100>.

¹¹⁷ “Army ants” should not be confused with “soldier ants”. The term “army ants” refers to a number of nomadic ant species which travel in columns; “soldier ants” refers to a caste suited to combat, found in many species of ant.

¹¹⁸ Jorge L P Souza and Carlos A R Moura, “Predation of Ants and Termites by Army Ants, *Nomamyrmex esenbeckii* (Formicidae, Ecitoninae) in the Brazilian Amazon” 52, no. 2 (2008): 5.

¹¹⁹ Hölldobler and Wilson, *The Ants*, 252.

¹²⁰ “Aggression in Wood Ants (*Formica polyctena* Foerst., Hymenoptera, Formicidae).”

¹²¹ Hölldobler and Wilson, *The Ants*, 261.

Slavery

If the adults of a “slave” colony do not resist the invasion and permit the theft of their brood they may be left unmolested. (There are even cases where the raiders physically pick up the adults of the raided species and place them to one side unhurt.) There is no mutual and lethal conflict in such instances so we must be cautious about speaking of war. On the other hand, if the invaded colony resists, battle will typically ensue. The resisters usually lose and in some cases are killed in large numbers.¹²² However, this is not always a one-sided massacre but can become an extended battle with great losses on both sides. Wheeler says, “the battle may continue for hours or even days” and “the ground may be strewn with the corpses of both species.”¹²³

War overlaps with both predation and slavery in the case of the Honey Pot ant, among which the living bodies of some individuals (“repletes”) are receptacles of nutritious substances. A colony that raids a neighbouring colony of the same species may seize, kill and eat the repletes. They may also capture other honey pot ants and incorporate them into their labour force.¹²⁴

What armies do

Law Professor Rosa Brooks wrote her recent book *How Everything Became War and the Military Became Everything* to emphasize how the boundaries of war in common usage have blurred.¹²⁵

Looking at the boundaries of war in the world of insects removes us emotionally from the conclusions we reach.

In the view of war as a system there are two concepts: “Wars” are events of mass, mutual, fatal, organized violence as we have defined here, and act as the “demand” of a war system, calling armies into existence. “Armies” engage in many activities: they produce wars, but not all of their activities are wars. Both “wars” and “the activities of armies” depend on the war system, but they may also overlap with other systems.

Consider the slave-taking raids described above. Even when mutual, lethal conflict does not ensue it is fair to speculate that the raided colony “knows”—in some sense of the word—of the destruction that likely awaits them if they resist; that they are “aware” of the force the invaders have at their command.

¹²² Wheeler, *Ants: Their Structure, Development, and Behavior*, 483–84.

¹²³ Wheeler, 462–63.

¹²⁴ Hölldobler and Wilson, *The Ants*, 414.

¹²⁵ Rosa Brooks, *How Everything Became War and the Military Became Everything* (Simon & Schuster, 2016), <https://www.simonandschuster.com/books/How-Everything-Became-War-and-the-Military-Became-Everything/Rosa-Brooks/9781476777870>.

If this is the case, successful slave-taking depends on the war system even when battles do not take place.

A human parallel would be the frequent cases where powerful imperial powers are able to pillage smaller countries. The smaller countries may let them get away with all sorts of crime and exploitation because they know of the robustness of the war system hosted by the raiders, even if it is, at a given moment, in its cold state.

If these speculations are on the right track, the existence of slavery, as a system hosted by *formicidae*, depends on the existence of the system we are calling war.

11. DISCUSSION

In this article a definition of war has been proposed that is intentionally broad, and that casts the net widely enough to include species other than *homo sapiens*. The tradition of conceiving of war as a system, combined with this broad definition of war, permits the uncovering of war as a system in the natural world.

Drawing lessons from ants in a simplistic sense ("consider the ant, thou sluggard") holds no attraction for scholars today, but we can still be stimulated to see and to think in new ways when we study systems common to humans and to life forms other than the human. The consideration of formic war allows old questions to be asked in new ways. Although it is beyond this article's scope to pursue this topic in detail, we conclude with some examples of questions that may benefit from the perspective outlined in this paper.

Symbiosis

Are there symbiotic relations between human beings and other life forms—as are found in some ant species—that increase the vigour of war as a system or magnify the violence of its hot state? Is it even possible that our technologically-generated prostheses, including advanced digital systems, have begun to play the role played in the formic world by species with symbiotic relations?

War triggers

How does the triggering process, whereby the cold state of war is replaced by the hot state, take place in humans? What role does physiology play, and what roles do culture and human rationality play? How are war triggers *manufactured* by those with a vested interest in the vigour of war?

The proper study of human war:

We have suggested in the article that attempting to study war while paying attention only to its hot state (by counting corpses, for example) is doomed to failure. But, if this is the case, what are the best ways of studying human war—of taking its temperature, assessing its vigour, predicting its future?

Human war—suppression versus weakening

When human war is kept largely in its cold state—let us say, by the curtailing of the arms trade or through the outlawing of "wars of aggression" (hot state trans-border incursions)—what are the long-term prospects for war? Does the entire war system eventually tend to wither away or can war, though kept in a cold state, swell in its deadly potential, waiting for the right war trigger to unleash its fury? Which are the effective and which are the ineffective ways of weakening war as it exists globally and systemically among human beings?

The superorganism

Ever since the nineteenth century it has been known that certain animal societies, including human societies, exhibit characteristics of an organism—an organism, that is, consisting of other, smaller organisms in complex relationship. Eusocial insects such as ants are obvious cases where societies appear to be such "superorganisms." The question thus arises: Does the system called war exist only where there is a superorganism? Is the hot state of war a mode of the superorganism, as this larger being fights for its life and well-being, not hesitating to sacrifice the individual organisms of which it consists for the greater whole?

Grey zone and spectrum of conflict theories

To conclude, we pursue one question in slightly more detail.

The definition of war used in this essay is incomplete. Mass, organized, mutual, and lethal conflict between communities is compatible with two ways of thinking about war and peace. One is to that war and peace are separate domains, with a relatively clear dividing line separating the two. As has been mentioned above, many human societies have independently developed ways to keep war and peace separate. Rituals, laws, and a separate warrior class all emphasize the fact that there are two sets of rules of behaviour: one set for war and one for peace. Killing, as an obvious example, is forbidden outside war. In the context of war, killing is not only permitted but may be mandated;

it is not condemned but may be glorified. And even in wartime, killing of civilians or captured soldiers may be forbidden.

Of course, like the coastline of an island, these boundaries are never absolutely sharp. Skirmishes take place that may not escalate to warfare, some killings may be permitted in peacetime, and so on. Yet the boundaries never fade away and war and peace, like the land and the sea, never fade into a mere continuum of wetness.

But military theorists have been pushing against this distinction, appealing to ideas of “grey zones” or intermediate states.¹²⁶

What do ants have to tell us about grey zones? They show that measures to draw a clear line – borders, us/them distinctions, triggering of recruitment and psychological changes, are not the result of sentimentality or wishful thinking, but are common across war as a system in nature. Bright lines are an essential part of limiting the damage caused by warfare, and fuzzy boundaries may be more war: wood ants, as we said above, fight wars after hibernation, when boundaries have been lost.

We have already seen that some ant species have gone in the other direction: Argentine ants, wood ants and others that have developed “supercolonies” with many nests and many queens have adopted a path of integration, maintaining peace between the nests by continual exchange of goods, organisms, and colony CHC odours. Yet even here, the arrangement is an all-or-nothing, with the supercolony prepared to engage in warfare with neighbouring supercolonies.

Such insights don’t “need” ants, of course. The importance of “bright lines” has long been known to scholars of war, and in his Nobel Prize speech Thomas Schelling turned to the idea again.¹²⁷ Yet seeing the importance played out in

¹²⁶ John Arquilla, “Perils of the Gray Zone: Paradigms Lost, Paradoxes Regained,” *PRISM* 7, no. 3 (2018): 118–29; Patrick Brady, “Between Peace and War: Gray Zone, Bright Line, or Dialectic? | RealClearDefense,” December 7, 2020, https://www.realcleardefense.com/articles/2020/12/07/between_peace_and_war_gray_zone_bright_line_or_dialectic_652193.html; Lyle Morris et al., *Gaining Competitive Advantage in the Gray Zone: Response Options for Coercive Aggression Below the Threshold of Major War* (RAND Corporation, 2019), <https://doi.org/10.7249/RR2942>; Donald Stoker and Craig Whiteside, “Blurred Lines: Gray-Zone Conflict and Hybrid War—Two Failures of American Strategic Thinking,” *Naval War College Review* 73, no. 1 (2020): 38; Brooks, *How Everything Became War and the Military Became Everything*, 352–53; Nadia Schadlow, “Research & Debate—It’s a Gray, Gray World,” *Naval War College Review* 73, no. 3 (2020): 7; Nadia Schadlow, “War and the Art of Governance,” *The US Army War College Quarterly: Parameters* 33, no. 3 (August 1, 2003), <https://doi.org/10.55540/0031-1723.2168>.

¹²⁷ Thomas C. Schelling, “An Astonishing Sixty Years: The Legacy of Hiroshima (Nobel Prize Speech)” (Nobel Foundation, 2005), <https://onlinelibrary.wiley.com/doi/abs/10.1111/nej.12236>.

this seemingly distant world of ants does emphasise its universality and its structural basis, separating it from mere “wishful thinking”.

Building a “spectrum of conflict” perspective into military strategy has been largely a unilateral effort from the American military and its theorists/strategists, advocated in part to give the military flexibility to combat non-state actors. Ants show us that it is not stable as an international perspective: there is no guarantee of universal peace, but maintaining a clear distinction between war and peace, and avoiding the slippery slope into “spectrum of conflict” and “grey zone” ideas is an important step.

12. CONCLUSIONS

Appreciating that qualities once thought to be uniquely human are found elsewhere in nature is often a valuable step in itself. Understanding that intelligence and language are not limited to humans has helped us better appreciate our place in the natural world. Perhaps there is something to be gained by appreciating that our complex societies too, with their achievements and tribulations, are not as unique as we once thought. Accepting that war is not limited to humanity is one small piece with the other adjustments we have made regarding our place in nature.

Ant wars show that human ingenuity is not essential to the development of social complexity, and humans are not the only species capable of developing the set of competences that warfare involves.

Treating war as a peculiarly human activity is particularly inaccurate because most of the wars fought on this planet have been insect wars and most of the deaths from war have been insect deaths. Almost all the fatalities of war are insects. Some insect wars are of long duration, with cumulative fatalities in the billions.

The variety of behaviours among ants is astonishing, and more subtleties and novelty continue to be discovered by myrmecologists’ careful observations and experiments. An obvious entry point to the idea of treating war as a system in nature is to ask whether we can use ant warfare to predict the outcome of human warfare. We consider this unlikely: as with other highly non-linear problems the range of possibilities is too great. Instead, we see potential for ant behaviour to provide a source of inspiration or “hypothesis generation” for those studying war in a human context, and hope that our suggestions and attempts in this essay may prompt others.

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